

smooth seeds, although both plants, *S. litoralis* and *S. crassicaulis*, are found in northern Japan, in their typical form. I came to the conclusion, considering the occurrence of several intermediate forms, that *S. litoralis* should be regarded as a geographical variety of *S. crassicaulis* and made the combination *S. crassicaulis* var. *littorea* (Makino) for the former in Journal of Japanese Botany XIII, p. 556 (1937). But now, as *S. maxima* A. Gray antedates Watson's name by 24 years, I must change the combination as follows.

*SAGINA MAXIMA* A. Gray, Bot. Jap. p. 382 (1859) in adnota. *S. Linnaei* Presl var. *maxima* (A. Gray) Maximowicz in Bull. Acad. Imp. Sc. St. Pétersb. XVIII, p. 372 (1873) pro parte; Matsumura, Ind. Pl. Jap. II-2, p. 86 (1912) pro parte. *S. maxima* f. *littorea* Makino in Bot. Mag. Tokyo XXV, p. 156 (1911). *S. litoralis* Hultén, Fl. Kamt. II, p. 78, fig. 8 (1928) and IV, p. 248 (1930); Komarov, Fl. Penin. Kamt. II, p. 102 (1929); Steinberg in Fl. URSS. VI, p. 473, t. XXV, fig. 7 (1936); Hultén, Fl. Aleut. p. 169 (1937). *S. crassicaulis* var. *littorea* (Makino) Hara in Journ. Jap. Bot. XIII, p. 556 (1937).

Var. **crassicaulis** (Watson), comb. nov. *Sagina crassicaulis* Watson in Proc. Amer. Acad. XVIII, p. 191 (1883); Hultén, Fl. Aleut. p. 168 (1937); Hara, l. c. (1937).

## II. THE CRUCIFEROUS GENUS PHYSARIA

REED C. ROLLINS<sup>1</sup>

(Plate 556)

THE Cruciferae are highly developed in western North America both as to the number of biological entities present and the extent of their divergence from any single morphological pattern. A number of genera, including *Physaria*, are unique in being wholly confined to this area and in that they are apparently of comparatively recent origin. These features together with the fact that *Physaria* has never been intensively examined make a study of certain aspects of its ecology, cytology, morphology, speciation and the relationships of its species seem highly desirable. With these points in mind, an investigation of the genus was undertaken involving detailed observations in the field and in the laboratory. The results are presented in the paragraphs that follow.

*Physaria* occurs in the Upper Sonoran, Transition, Montane and lower Canadian life-zones, chiefly on high plateaus and lower moun-

<sup>1</sup> Society of Fellows of Harvard University.



tain elevations, from the great plains to the Cascades and Sierra Nevada and from Canada to Arizona and New Mexico. In general the habitat is of a dry barren sort, where sunlight is intense and competition between plant species and individuals often approaches a minimum, but where survival entails special adaptation. The xeric conditions under which the plants survive is reflected in the abundant, often densely encrusted vestiture found upon them. Though the Cruciferae have long been famous for the lime-preference which its members show, *Physaria*, as is true of several other genera in the family, seems to be somewhat less selective. This is particularly true of certain species. The plants often occupy siliceous soils of a loose nature or are equally at home on heavily lime-impregnated shale outcrops.

The natural relationship between *Physaria* and *Lesquerella* is very marked. These two genera have almost exactly the same floral pattern, habit of growth and vestiture, which is of a distinctive sort. The siliques too are very similar. In fact the two are not easily recognized as distinct genera if only flowering plants are considered. The fruit of *Physaria* is always didymous, markedly constricted at the replum and usually highly inflated, while that of *Lesquerella* is unconstricted at the replum, never didymous and much less inflated. But even in these respects certain species of *Lesquerella*, namely *L. Kingii* and its close relatives, approach the condition found in such species of *Physaria* as *P. Geyeri*. This relationship was pointed out by Payson,<sup>1</sup> but was disregarded or overlooked by O. E. Schulz<sup>2</sup> who recently placed the two genera in widely separated tribes of the family. The cytological evidence also indicates a closer relationship than that attributed to them by Schulz. On the other hand there is no question as to the separateness of these two genera.

Three species of *Physaria* have been investigated cytologically, the chromosome number having been found to be  $N = 4$  in each case (text figs. 1 & 2). These counts, the first for the genus, were made from aceto-carminic smears of developing pollen. Buds from wild plants were killed and fixed in alcohol-acetic in the field at the following localities: *P. acutifolia* Rydb.,  $N = 4$ , dry hillsides, granitic talus, 5 mi. east of Parlin, Gunnison Co., Colo., May 21, 1938, *Rollins* 2088 (G, R); *P. floribunda* Rydb.,  $N = 4$ , dry rocky hillside, 3 mi. east of

<sup>1</sup> Ann. Mo. Bot. Gard. 8: 129 (1921).

<sup>2</sup> Natur. Pflanzenfam. 17b (1936).



Sapinero, Gunnison Co., Colo., May 23, 1938, *Rollins 2108* (G, R); *P. australis* (Pays.) Rollins,  $N = 4$ , limy knoll, 3 mi. west of Fort Bridger, Uinta Co., Wyoming, *Rollins 2229* (G, R). If these results may be taken as indicative, then the basic or fundamental number for *Physaria* must be four.

It has been suggested by Payson (*l. c.*) that *Physaria* was derived from *Lesquerella*. His suggestion was based chiefly on morphological studies, but is equally supported by the present cytological observations on both genera. Chromosome numbers of  $2N = 10$ , 18 and 12 have been reported for *Lesquerella* by Manton.<sup>1</sup> I have found  $N = 5$  for four species,  $N = 6$  for one species and  $N = 8$  for another species

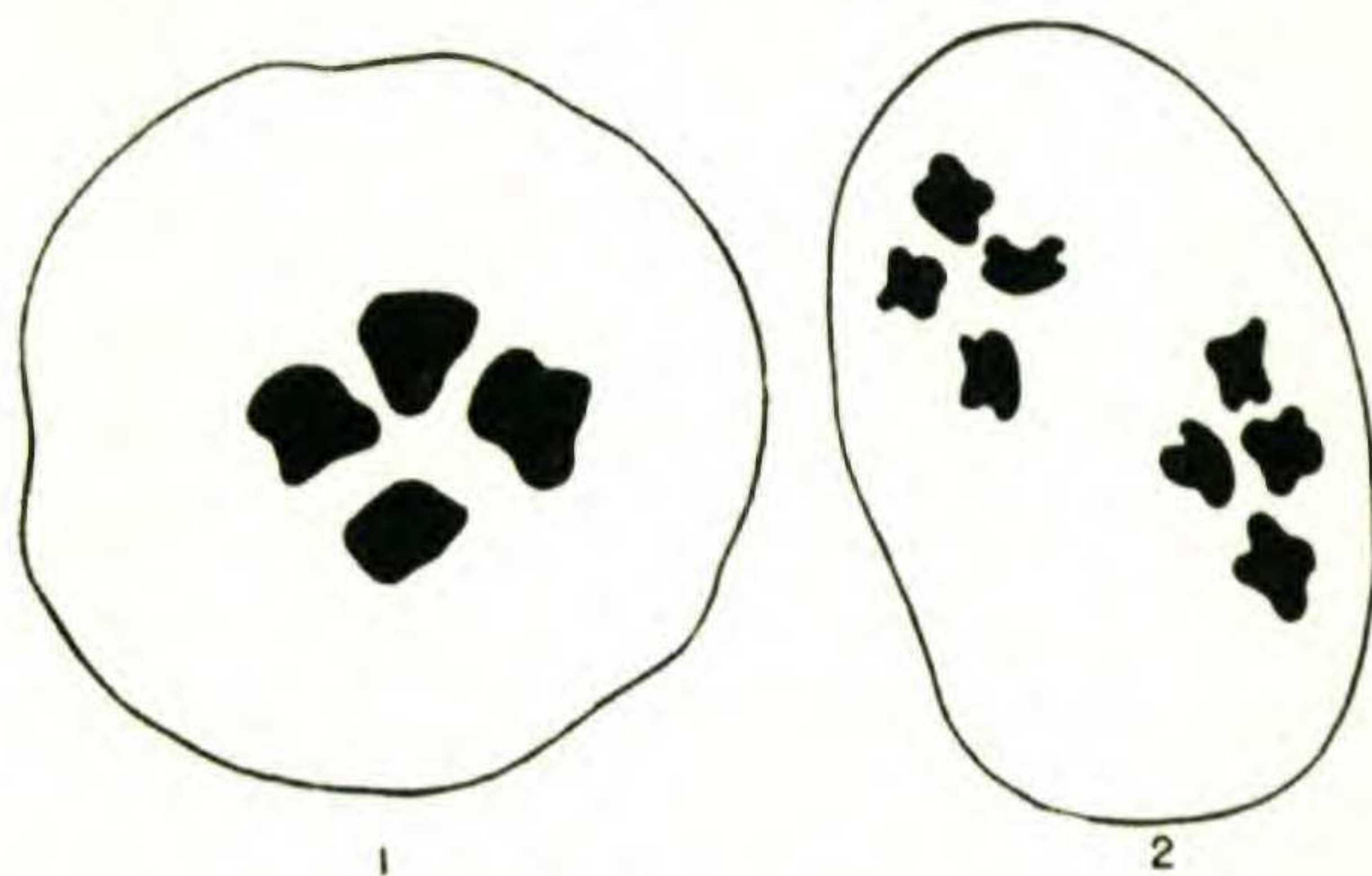


FIG. 1. Chromosomes in a developing pollen grain of *PHYSARIA FLORIBUNDA* Rydb. *Rollins* no. 2108.  $\times$  about 1000.

FIG. 2. Chromosomes in a dividing pollen mother cell of *P. ACUTIFOLIA* Rydb. *Rollins* no. 2088.  $\times$  about 1000.

of the same genus.  $N = 5$  and 6 coincide with the findings of Manton, but the discovery of  $N = 8$  further indicates a probable aneuploid relationship between species of the genus. A cytological study of *Lesquerella* has not proceeded far enough for the accurate determination of its basic chromosome number, but since  $N = 5$  is lowest and most commonly found, in all probability, it represents one of the fundamental numbers for the genus. If this is true, then the case of *Physaria* and *Lesquerella* may be added as a further example of the aneuploid relationship between genera of the Cruciferae so lucidly described by Manton. In any case it seems probable that the loss of a single chromosome from the complement of five found in certain members of *Eu-Lesquerella* has been of major importance in the genesis of *Physaria*.

Several inter-related groups of species are found in *Physaria*, but

<sup>1</sup> Ann. Bot. 46: 531 (1932).



none are sufficiently distinct and definable to make necessary or desirable a subdivision of the genus. In fact each is connected with another through a continuous chain of intermediate species. Probably the most natural aggregation is that made up of *P. Geyeri*, *P. oregona*, *P. alpestris* and *P. Newberryi*. Of these, the former two species show a closer relationship between one another than with either of the latter two. The following may be noted as characteristics commonly shared by members of this group: shallow apical sinus, ovate to ovate-lanceolate replum with an acute apical angle, valves compressed opposite the replum-axis and the lack of a basal sinus. The ovule-number ranges from 2 to 6 in each loculus of the silique among members of this group. There is apparently a straightforward evolutionary trend expressed among these species which becomes increasingly evident when the structural relationships of the fruits are thoughtfully considered. The most striking changes have apparently accompanied a reduction in the number of ovules. These include a progressive sterilization of ovuliferous tissue along the outer margins of the replum. This tissue when relieved of its ovule-bearing function appears to have been converted into tissue of the style. The result has been a shortening of the replum and an increase in the length of the style. If one attempts to arrange the species of this group in a probable evolutionary sequence, invariably *P. oregona* comes out as the most primitive. From the primitive stock, *P. Geyeri* and *P. alpestris* appear to be direct descendants. The genesis of *P. Newberryi* may be the same, but the relationship here is not quite so evident. *P. Chambersii* seems to be transitional toward other members of the genus. Its silique has certain features in common with *P. alpestris*, but the replum resembles that of *P. floribunda*.

Another natural grouping includes *P. didymocarpa*, *P. condensata* and *P. australis*. Here as in the above we see a progressive reduction in ovule-number, lengthening of style and shortening of replum which results in a greater constriction between the valves. Several types of divergence from the primitive *P. didymocarpa* are notable. *P. condensata* shows the extreme in reduction of growth-form and must surely be a derived species. Another divergence is found in *P. didymocarpa* var. *lanata* in which the entire body of the plants is invested in the same loose pubescence characteristic of only the silique in the species proper. The number of ovules in each ovary-loculus has been reduced to two and the replum has become exceedingly short and



constricted in *P. australis*. This species appears to be the natural link to the third group of inter-related species to which *P. vitulifera*, *P. Osterhoutii*, *P. brassicoides*, *P. acutifolia*, *P. floribunda* and *P. Grahamii* belong. These species all possess moderately inflated siliques and the ovule-number is uniformly two for each loculus of the ovary. No very marked evolutionary trends are evident, hence any attempt to arrange the species according to the probable order of their origin would be little short of pure speculation. However, certain of the species are more closely related than others. For example, *P. vitulifera* and *P. Osterhoutii* are obviously closely inter-related as are also *P. floribunda* and *P. acutifolia*.

All the known species of *Physaria* are perennial and possess a relatively large central tap-root. The plants are caespitose, with herbaceous flowering stems arising laterally on an elongated woody, usually simple caudex. The basal leaves are borne along the caudex and subtend the flowering stems. These leaves invariably form a sterile rosette on the terminal portion of the caudex or caudex-branch, imparting a characteristic symmetry to the plants as they are observed in their native habitats. This rosette-habit is found in its extreme form in *P. condensata*, where most of the plant is simply "rosette." The shape, size and degree of tothing of the leaves varies between species, but there is a certain amount of stability on these features within any given entity. There is a tendency for the leaves to be entire, or at most remotely dentate, in most species of the genus. However, certain species have the basal leaves dissected.

The flower-parts are reasonably uniform throughout the genus and offer little of diagnostic value in distinguishing between species. The sepals are recognizable as two pairs, one being broader than the other. They are always pubescent with the same type of indument which is found on the rest of the plant. The petals are glabrous, entire, yellow and nearly spatulate. There is little differentiation between blade and claw, but the two pairs of petals differ in width. Characters of the fruit are highly important in indicating relationships and are extremely useful in the delimitation of natural entities. This point was adequately emphasized by Robinson<sup>1</sup> who said of *Physaria*, "species with excellent characters in the fruit, but otherwise very difficult to distinguish." The siliques are pubescent, didymous, variously shaped and possess a sinus at both base and apex or at apex only. The replum

<sup>1</sup> Syn. Fl. 1: 121 (1895).



is an important diagnostic character which has previously been almost entirely overlooked. Shape, apical angle and dimensions are all important considerations. The number of ovules in each loculus of the silique is a constant feature of several species. This constancy seems to be correlated with a reduced number. Abortion is so common in *Physaria* that it is the normal condition. Species with four or more ovules in each loculus normally develop two or three seeds and species with two ovules in each loculus usually develop only a single seed. The style is persistent and varies in length, but within limits the style is a useful character for distinguishing certain species.

The seeds are wingless and fairly uniform throughout the genus, differing only in dimensions. Within the seeds, the cotyledons are consistently accumbent. The indument varies only slightly, being always of the many-rayed stellate type. The rays are nearly always forked, but vary in length and the degree to which they are appressed to the plant-surface. In *P. Grahamii* and *P. didymocarpa* var. *lanata* the stellae are sufficiently long and spreading to give a lanate appearance to the plants. Uniform in type, covering the entire mature plants and nearly always giving them a silvery appearance, the vestiture cannot be considered of major importance in specific delimitation as is the case in many genera of the Cruciferae. Plants of *Physaria* have been grown in a greenhouse where observations were made on their ontogenetic development. In a young plant the cotyledons are perfectly glabrous, strikingly in contrast with the first pair of true leaves which are heavily incrustated with stellae. In general habit plants grown under artificial conditions differ in no marked way from those which one observes in nature.

Nuttall is credited with the recognition of *Physaria* as a distinct entity by his having been listed as the author of section *Physaria* of the genus *Vesicaria* by Torrey and Gray.<sup>1</sup> After the publication of a second species in the group by Hooker,<sup>2</sup> Gray<sup>3</sup> realized that the plants belonged to a different genus and accordingly raised section *Physaria* to generic rank and at the same time transferred *Vesicaria didymocarpa* and *V. Geyeri* to it. The generic status of *Physaria* as a biological category has never been questioned by subsequent workers. O. Kuntze<sup>4</sup> substituted the name *Coulterina* for *Physaria*, contending

<sup>1</sup> Fl. North Am. 1: 102 (1838).

<sup>2</sup> Lond. Journ. Bot. 6: 70 (1847).

<sup>3</sup> Gen. Illustr. 1: 162 (1848).

<sup>4</sup> Revis. Gen. 2: 931 (1891).



that the fungus genus *Physarium* preoccupied the name. However, no such interpretation is possible under specific provisions of the International Rules of Botanical Nomenclature. *Physaria* has been studied in parts by the writers of manuals on the botany of western America, but the nearest approach to an inclusive treatment of the genus is that of Payson,<sup>1</sup> in which a key and notes on the distribution of the species are presented.

It is a pleasure to acknowledge unreserved cooperation from the following public or private herbaria in connection with this study: Clokey Herbarium (Cl); Gray Herbarium (G); New York Botanical Garden (NY); North Dakota Agricultural College (NDA); Rocky Mountain Herbarium (RM); United States National Herbarium (US). Collections bearing the symbol (R) are in my own herbarium.

#### SYNOPSIS OF THE GENUS *PHYSARIA* (Nutt.) Gray

Perennial, caespitose, silvery stellate; stems simple, arising laterally on a somewhat elongated caudex; basal leaves usually numerous, often terminating the caudex or its branches in rosette, form, petiolate, oblanceolate to obovate or the blade rotund, entire, dentate or divided into segments; cauline leaves present, usually few, entire or dentate; inflorescence congested to somewhat elongated, usually elongating in fruit; pedicels rigid; sepals linear-oblong, pubescent, often cucullate at apex; petals yellow or rarely purplish, usually spatulate, glabrous; siliques didymous, pubescent, often highly inflated, apical sinus present; ovules 2-6 in each loculus; style persistent; seeds brown, wingless.—Gray, Gen. Illustr. 1: 162 (1848); Coulter, Man. Rky. Mt. Region 26 (1885); Prantl in Engler & Prantl, Nat. Pflanzenfam. 3: 187 (1891); Robinson in Gray, Syn. Fl. N. Am. 1: 121 (1895); Howell, Fl. Northw. Am. 1: 52 (1897); Britt. & Brown, Ill. Fl. 2: 135 (1897); Heller, Cat. N. Am. Pl. 88 (1900); Rydb., Fl. Colo. 154 (1906); Coulter & Nelson, Man. Cent. Rky. Mts. 217 (1909); Hayek in Beih. Bot. Centr. 27: 311 (1911); Frye & Rigg, Northw. Fl. 186 (1912); Piper & Beattie, Fl. Se. Wash. and Adj. Ida. 121 (1914); Clements & Clements, Rky. Mt. Fls. 25 (1914); Wootton & Standley in Contrib. U. S. Nat. Herb. 19: 270 (1915); Rydb., Fl. Rky. Mts. Adj. Pl. 330 (1917); Payson in Ann. Mo. Bot. Gard. 5: 143 (1918); Tidestrom in Contrib. U. S. Nat. Herb. 25: 233 (1925); Rydb., Fl. Pr. Pl. Centr. N. Am. 362 (1932); Munz, Man. So. Calif. Bot. 197 (1935); St. John, Fl. Se. Wash. Adj. Ida. 175 (1937). *Coulterina* O. Kuntze, Revis. Gen. 2: 931 (1891). *Vesicaria*, sect. *Physaria* Nutt. ex Torr. & Gray, Fl. N. Am. 1: 102. (1838). TYPE SPECIES: *P. didymocarpa* (Hook.) Gray.

<sup>1</sup> Ann. Mo. Bot. Gard. 5: 143-147 (1918).



## ARTIFICIAL KEY TO THE SPECIES

- a. Style less than 3.5 mm. long (usually 1–2 mm.); replum lanceolate; basal sinus absent....*b.*
  - b. Valves of silique slightly inflated, flattened contrary to replum, not keeled; apical sinus and sinus-shoulders rounded.....1. *P. oregona.*
  - b. Valves of silique highly inflated, strongly keeled on margins; apical sinus and sinus-shoulders acute.....4. *P. Newberryi.*
- a. Style more than 4 mm. long; replum various, but lanceolate only in *P. alpestris*; basal sinus present or absent....*c.*
  - c. Apical sinus of silique shallow (less than 1 mm.); apical angle of replum acute (except in *P. Geyeri* var. *purpurea*)....*d.*
    - d. Silique slightly inflated, cordate in outline, less than 1 cm. wide; ovules 2 in each loculus (sometimes 3 in var. *purpurea*).....2. *P. Geyeri.*
    - d. Silique highly inflated, orbicular in outline, more than 1 cm. wide; replum lanceolate; ovules about 4 in each loculus.....3. *P. alpestris.*
  - c. Apical sinus of silique deep (more than 2 mm.); apical angle of replum obtuse....*e.*
    - e. Replum obovate; ovules 4 in each loculus of silique....*f.*
      - f. Basal leaves 5–15 mm. long; plants densely tufted; stems less than 1 cm. long.....7. *P. condensata.*
      - f. Basal leaves 15–40 mm. long; plants loosely tufted; stems about 1 dm. long.....6. *P. didymocarpa.*
- e. Replum narrowly oblong to linear-oblong (broader in *P. acutifolia* but there are only two ovules in each loculus in this species); ovules 2–6 in each loculus of silique....*g.*
  - g. Sinuses of silique equal above and below; valves nearly orbicular.....8. *P. australis.*
  - g. Sinuses of silique unequal (upper very deep, lower shallow or absent); valves variously shaped but not orbicular....*h.*
    - h. Silique highly inflated, 1.5–3 cm. wide; valves membranaceous.....5. *P. Chambersii.*
    - h. Silique moderately inflated, less than 1.5 cm. wide; valves coriaceous....*i.*
      - i. Plants loosely pubescent (almost lanate); cauline leaves dentate.....9. *P. Grahamii.*
      - i. Plants closely appressed-pubescent; cauline leaves entire....*j.*
        - j. Basal leaves rounded at apex; apical sinus of silique broad and deep (equaling replum-length in width and depth)....*k.*
          - k. Silique cordate, acute at base; basal leaves large (about 2 cm. broad).....10. *P. brassicoides.*
          - k. Siliques rectangular in outline, obtuse or truncate at base; basal leaves smaller (about 1 cm. broad) .....11. *P. vitulifera.*
        - j. Basal leaves acute at apex; apical sinus of silique shallow or narrow and deep....*l.*
          - l. Apical sinus of silique narrow (less than 1 mm.) and deep (equaling replum-length); basal sinus absent; siliques pendant, loosely stellate.....12. *P. Osterhoutii.*
          - l. Apical sinus of silique broad (more than 2 mm.); basal sinus usually present but very



shallow; siliques erect or pendant, appressed-pubescent. . . . *m.*

- m. Basal leaves entire or with a single broad tooth on each side, linear-oblongate, less than 4 cm. long; replum narrowly obovate. . . . . 13. *P. acutifolia.*
- m. Basal leaves divided, broadly oblongate, more than 4 cm. long; replum linear, constricted. . . . . 14. *P. floribunda.*

1. *P. OREGONA* Watson. Perennial, caespitose, silvery stellate-pubescent throughout; caudex simple; stems several to numerous, erect or somewhat decumbent, simple, 1–3.5 dm. long including the fruiting raceme; basal leaves obovate, slender-petioled, usually incised or with a few broad teeth along the petiole, 4–6 cm. long, 8–15 mm. broad; cauline oblongate or broader, entire or sparsely dentate, acute, 1.5–2.5 cm. long, 3–5 mm. wide; sepals pubescent, oblong, 5–7 mm. long, about 1 mm. wide; petals lemon-yellow, spatulate, 9–12 mm. long, 2–3 mm. wide; fruiting pedicels spreading, curved upward, 1–2 cm. long; fruiting raceme 5–15 cm. long; siliques didymous, loosely pubescent with spreading stellae, inflated but not exceedingly so, flattened laterally, obreniform, 1.8–2.5 cm. broad, 10–12 mm. long; apical sinus broad and open, basal sinus lacking; replum broadly lanceolate, acute at apex, 6–8 mm. long, 2–3 mm. wide; style 1–2 mm. long; ovules 4 on each side of replum; seeds orbicular, brown, 2–3 mm. broad, 2–3 in each loculus, marginless.—Proc. Am. Acad. Arts & Sci. 17: 363 (1882); Robinson in Gray, Syn. Fl. 1: 121 (1895); Howell, Fl. Northw. Am. 1: 52 (1897); Frye & Rigg, Northw. Fl. 186 (1912); Payson in Ann. Mo. Bot. Gard. 5: 146 (1918); St. John, Fl. Se. Wash. Adj. Ida. 175 (1937). *Coulterina oregona* O. Kuntze, Revis. Gen. 2: 931 (1891).—Western Idaho and eastern Oregon. IDAHO: Sheep Creek, Snake River Canyon, Idaho Co., April, 1935, *Constance & Rollins 1029* (NY); May, 1937, *Constance, Hedrick & Peters 1822* (G, R). OREGON: Pine Creek, Baker Co., June 23, 1880, *Cusick* (G TYPE, US ISOTYPE); April, 1881, *Cusick* (G); 1886, *Cusick* (G, US); hillsides near Snake River, May 25, 1898, *Cusick 1895* (G, US); near Imnaha, Wallowa Co., July, 1933, *Peck 17500* (NY); Cache Creek, Wallowa Co., May, 1897, *Sheldon 8183* (G, NY, US).

The outstanding distinctive characteristics of *P. oregona* are found in the silique, which is flattened contrary to the replum and only slightly inflated laterally. In these respects the species is similar to *P. Geyeri* and differs from other members of the genus. The larger silique and shorter style easily differentiate it from the latter species. *P. oregona* is an endemic of the Snake River Canyon region of Oregon and Idaho and is of interest because of its restriction to this unique area.<sup>1</sup>

<sup>1</sup> See Constance & Rollins, Proc. Biol. Soc. Wash. 49: 147 (1936).



2. *P. GEYERI* (Hook.) Gray, var. **typica**. Perennial, caespitose, silvery stellate-pubescent throughout; caudex usually simple; stems numerous, decumbent, simple, arising laterally, 1–3 dm. long including the fruiting raceme; basal leaves numerous, obovate, slender-petioled, entire or rarely with a few broad teeth along the petiole, 3–7 cm. long, 8–12 mm. broad; cauline entire, oblanceolate, 1.5–3 cm. long, 3–5 mm. wide; sepals oblong, pubescent with spreading stellae, 5–7 mm. long, 1–2 mm. wide; petals yellow, spatulate, 8–12 mm. long, 3–4 mm. wide; pedicels spreading, slightly curved upward or sigmoid, 1–2 cm. long; siliques didymous, inflated but not exceedingly so, obcordate, apical sinus broad and open, basal sinus absent, loosely pubescent with spreading stellae, flattened laterally, 6–9 mm. broad, 5–7 mm. long; replum ovate, apical angle acute, 4–6 mm. long, 2–3 mm. broad; style 5–7 mm. long; ovules 2 in each loculus; seeds brown, marginless, 1 or 2 in each loculus, about 2 mm. broad.—*P. Geyeri* (Hook.) Gray, Gen. Illustr. 1: 162 (1848); Robinson in Gray, Syn. Fl. 1: 121 (1895); Howell, Fl. Northw. Am. 1: 52 (1897); Frye & Rigg, Northw. Fl. 186 (1912); Piper & Beattie, Fl. Se. Wash. Adj. Ida. 122 (1914); Rydb., Fl. Rky. Mts. Adj. Pl. 331 (1917) in part; Payson in Ann. Mo. Bot. Gard. 5: 146 (1918); St. John, Fl. Se. Wash. Adj. Ida. 175 (1937). *Vesicaria Geyeri* Hook., Lond. Journ. Bot. 6: 70 (1847). *Coulterina Geyeri* O. Kuntze, Revis. Gen. 2: 931 (1891).—Eastern Washington to western Montana. MONTANA: Jefferson Co., July, 1892, *F. D. Kelsey* (NY); Deer Lodge Valley, June, 1906, *M. E. Jones* (US); Madison Co., June, 1888, *F. Tweedy* (NY); Miller Creek, Missoula Co., May, 1926, *Kirkwood 2414* (G). IDAHO: shore of Lake Coeur d'Alene, Kootenai Co., July, 1895, *Leiberg 1314* (G, NY). WASHINGTON: Spokane Valley, *Geyer 476* (G isotype); Spokane River, Spokane Co., May, 1937, *Constance 1834* (G, R); June 1893, *Henderson 2384* (G); May, 1924, *St. John 7632* (G, NY); May, 1896, *Piper 2293* (G, NY); Hangman Cr., Spokane Co., May, 1893, *Sandberg & Leiberg 17* (G, NY); between Spokane River and Colville, Wilkes U. S. Explor. Exp. 435 (NY); Davenport, Lincoln Co., May 20, 1905, *M. E. Jones* (US).

The specific nature of this entity has not been questioned since its original publication by Hooker. As pointed out above, its natural relative is *P. oregona* from which it is amply distinct. *P. Geyeri* has a restricted geographical range and is apparently common in the Spokane Valley of eastern Washington where it was first discovered.

Var. **purpurea**, var. nov. Petals purple; apical angle of replum obtuse; ovules often 3 in each loculus of the silique.—Planta perennis; petalis purpureis; reple obovato basi apicique obtuso; loculis circa 3-ovulatis.—IDAHO: Bonanza, Custer Co., July 25, 1916, *Macbride & Payson 3448* (G TYPE, NY ISOTYPE); Challis Creek, Custer Co., July 1916, *Macbride & Payson 3342* (G, NY).

3. *P. ALPESTRIS* Suksdorf. Perennial, caespitose, silvery stellate-pu-



bescent throughout; caudex simple or rarely branched, stems several, simple, arising laterally, erect or somewhat decumbent, 5–15 cm. long including fruiting raceme; basal leaves numerous, entire, obovate, rarely acutish, tapering abruptly to a slender petiole, 3–5 cm. long, 1–2 cm. broad; cauline oblanceolate, few, 5–15 mm. long, 3–5 mm. broad; inflorescence subcorymbose; sepals oblong, pubescent, 8–10 mm. long, 1.5–2 mm. broad; petals yellow, spatulate, undifferentiated into blade and claw, 12–14 mm. long, 2–3 mm. broad; ovary incrustated with stellae; fruiting pedicels divaricate, straight, 5–10 mm. long; siliques didymous, highly inflated, with a shallow open sinus above, slightly notched below, evenly pubescent; valves subreniform, 1–1.5 cm. long, 7–10 mm. wide; replum lanceolate, acutely angled at apex, 7–10 mm. long, 1.5–2.5 mm. broad; style 5–7 mm. long; ovules 4–5 in each loculus; seeds brown, suborbicular, flattened, 2–3 mm. broad, 1–3 in each loculus.—West Am. Sci. **15**: 58 (1906); Payson in Ann. Mo. Bot. Gard. **5**: 147 (1918); G. N. Jones in Univ. Wash. Publ. **7**: 91 (1938). *P. didymocarpa* Howell, Fl. Northw. Am. **1**: 52 (1897) in part; Frye & Rigg, Northw. Fl. 186 (1912).—West-central Washington. WASHINGTON: locality uncertain, Wilkes U. S. Expl. Exp. 888 (NY, US); Mt. Stuart region, Chelan Co., Aug., 1930, *Thompson 5813* (G); Tronson Ridge, Chelan Co., June, 1932, *Thompson 8595* (G, NY); June, 1933, *Thompson 8966* (G, NY); Three Brothers, Chelan Co., June, 1934, *Thompson 10540* (NY); Beverly Creek, Kittitas Co., July, 1932, *Thompson 8708* (G, NY); near Liberty, Kittitas Co., June, 1935, *Thompson 11578* (G, NY); Mount Paddo (Adams), July 12, Sept. 2, 1900, *Suksdorf 2648* (G, NY isotypes); Aug. 30, 1904 and July 27, 1906, *Suksdorf 4137* (G).

*P. alpestris* has been critically discussed elsewhere. It stands well apart as a species both on morphological and geographical grounds. The nearest relative from a technical standpoint appears to be *P. oregona*, but the species is also related to *P. Chambersii* on account of the large highly inflated fruits and orbicular entire basal leaves. However, the replums of the two are decidedly different and it seems probable that their ancestry was entirely different.

4. *P. NEWBERRYI* Gray. Perennial, caespitose, silvery-stellate throughout; caudex simple or branched; stems several to numerous, erect, simple, arising laterally, 0.5–1 dm. long including the fruiting raceme; basal leaves obovate, incised or merely dentate with broad teeth, slender-petioled, 4–8 cm. long, 1.5–2.5 cm. broad; cauline few, entire, oblanceolate, 1–2 cm. long, 3–4 mm. wide; sepals linear-oblong, pubescent, 7–9 mm. long, about 1 mm. wide; petals yellow, ligulate, often truncate at apex, 10–13 mm. long, 2–3 mm. wide; fruiting raceme dense, 3–5 cm. long; pedicels rigid, straight, divaricate, 5–10 mm. long; siliques didymous, highly inflated, apical sinus broad the shoulders angular, evenly covered with appressed stellae; valves



keeled on both outer margins, each valve 8–12 mm. wide, 12–16 mm. long; replum linear, acute at apex, 8–10 mm. long, 1–1.5 mm. wide; style 2–3 mm. long; ovules 2–4 in each loculus; seeds obovate, light brown, marginless, 2–3 mm. wide, 3–4 mm. long.—Ives' Report Colo. River, pt. 4. 6 (1860); Robinson in Gray, Syn. Fl. 1: 121 (1895) in part; Coulter & Nelson, Man. Cent. Rky. Mts. 218 (1909) in part; Wootton & Standley in Contrib. U. S. Nat. Herb. 19. 270 (1915); Rydb., Fl. Rky. Mts. Adj. Plains 331 (1917) in part; Payson in Ann. Mo. Bot. Gard. 5: 146 (1918). *P. didymocarpa* var. *Newberryi* Jones in Proc. Calif. Acad. Sci. 2: 5. 624 (1895) in part. *Coulterina Newberryi* O. Kuntze, Revis. Gen. 2: 931 (1891).—New Mexico to northern Arizona. NEW MEXICO: locality uncertain, western New Mexico, May, 1869, *E. Palmer* (G, NY, US); near Tegua, May 14, 1858, *J. S. Newberry* (G TYPE, NY, US ISOTYPES); Fort Wingate, 1882 & 1883, *W. Mathews* (G); May 27, 1883, *C. D. Walcott* 43 (US); Gallup, June 14, 1916, *Eastwood* 5595 (G, US). ARIZONA: Cave Dwellers Mt., east of Mt. Agassiz, Aug., 1884, *Lemmon* 3356 (G); Sunset Peak, Flagstaff, June, 1928, *Osterhout* 7000 (RM); July, 1923, *H. C. Hansen* 620 (RM); July, 1937, *R. E. Collom* 746 (US); May–Oct., 1900, *Purpus* 7075 (US); July, 1901, *Leiberg* 5699 (US); 15 miles no. of Granado, Apache Co., June, 1937, *Peebles & Smith* 13478 (US); San Francisco Mts., June, 1887, *E. A. Mearns* (NY); near Flagstaff, June, 1891, *McDougal* 154 (US).

*Physaria Newberryi* is one of the most distinctive species of the genus and it is, therefore, difficult to understand why confusion over its relationship to other members has been so general. It would seem from the identifications on many specimens that any plant with highly inflated siliques, regardless of other characteristics, has been considered to be good *P. Newberryi*. Actually the V-shaped apical sinus, short style and straight-sided siliques are distinctive characteristics which well define this species.

5. *P. Chambersii*, sp. nov. Herba perennis caespitosa undique indumento argenteo-stellato tecta; caulibus decumbentibus vel erectis 5–15 cm. longis; foliis radicalibus obovatis vel rotundatis integris vel dentatis 3–6 cm. longis, 1–2 cm. latis; foliis caulinis integris spathulatis acutis 1–2 cm. longis, 3–6 mm. latis; inflorescentiis laxis; sepalis lineari-oblongis 6–8 mm. longis, 1 mm. latis; petalis flavis spathulatis 10–12 mm. longis, 3–4 mm. latis; pedicellis fructiferis divaricatis 8–15 mm. longis; siliquis didymis inflatis pubescentibus; loculis subreniformibus 1–1.5 cm. longis, ca. 1 cm. latis; replo oblongo 4–6 mm. longo, 1 mm. lato; stylo 6–8 mm. longo; loculis di- vel hexispermis; seminibus exalatis.

Perennial, caespitose, silvery stellate throughout; stems numerous from a simple caudex, arising laterally, erect or very often decumbent, simple, 5–15 cm. long including the fruiting raceme; radical leaves



entire or dentate, obovate to orbicular, slender-petioled, 3–6 cm. long, 1–2 cm. broad; cauline few, entire, spatulate, often acute, 1–2 cm. long, 3–6 mm. wide; inflorescence rather lax; sepals linear-oblong, pubescent, 6–8 mm. long, 1 mm. wide; petals yellow, spatulate, 10–12 mm. long, 3–4 mm. wide; fruiting raceme congested, 2–10 cm. long; pedicels divaricate, slightly sigmoid, 8–15 mm. long; siliques didymous, greatly inflated, evenly and often densely pubescent, often purplish at maturity, obtuse to slightly cordate at base; apical sinus deep and open, crests rounded; valves subreniform, each valve 1–1.5 cm. long, about 1 cm. wide; replum oblong, obtuse at apex, 4–6 mm. long, 1 mm. wide; style 6–8 mm. long; ovules 2–6 (mostly 4) on each side of the replum; seeds orbicular, flattened, brown, 2–3 mm. broad, 2–4 in each loculus, marginless.—*P. didymocarpa* Howell, Fl. Northw. Am. 1: 52 (1897) in part. *P. Newberryi* Rydb., Fl. Rky. Mts. Adj. Pl. 331 (1917) in part; Tidestrom in Contrib. U. S. Nat. Herb. 25: 233 (1925) in part; Munz, Man. So. Calif. Bot. 198 (1935).—Utah and Nevada. UTAH: Pahvant Butte, Millard Co?, May, 1925, *A. J. Harris C2518* (G); southern Utah, 1877, *E. Palmer 34* (NY, US); Thistle Junction, June, 1900, *S. G. Stokes* (NY, US); Cedar City, May, 1894, *M. E. Jones 5202* (NY, US); Marysvale, June, 1894, *M. E. Jones 5397c* (NY, US); Ephraim, San Pete Co., May, 1914, *Eggleston 10111* (US); Mt. Nebo, Juab Co., Aug., 1905, *Rydberg & Carleton 7701* (NY); Parley's Canyon, Salt Lake Co., June, 1923, *Garrett 3031* (G). NEVADA: Clover Mts., July, 1893, *E. L. Greene* (NY); Santa Rosa Mts., Humboldt Co., July, 1898, *Cusick 2025* (G, US); Lamoille Canyon, Ruby Mts., Elko Co., July, 1938, *Rollins & Chambers 2568* (G, R); Aug., 1908, *Heller 9378* (NY, US); 36 mi. w. of Wendover, Elko Co., June, 1934, *Maguire 5808* (G); 20 mi. sw. of Jiggs, Eureka Co., July, 1938, *Rollins & Chambers 2543* (G, R); mountain slopes of Jet Canyon, 15 mi. west of Round Mountain, Toiyabe Mts., Nye Co., July, 1938, *Rollins & Chambers 2502* (G TYPE, R ISOTYPE); Bunker Hill, Toiyabe Forest, July, 1913, *A. E. Hitchcock 860* (US); Trail Canyon, White Mts., Esmeralda Co., July, 1932, *Duran 3349* (G, NY); Mt. Gabb, Palmetto Range, 1898, *Purpus 5863* (US); Karshaw, Lincoln Co., May, 1902, *Goodding 973* (G, NY); Kyle Canyon, Charleston Mts., July, 1936, *Clokey 7102* (R, Cl); Clark Canyon, Charleston Mts., May, 1936, *Clokey & Anderson 7099* (R, Cl); Cold Cr., Charleston Mts., June, 1938, *Clokey 7946* (Cl). OREGON: Sheaville, Malheur Co., June, *Percy Train* (US) (This is a flowering specimen which is provisionally placed here. Certainly it is not *P. oregona* Wats. as determined by the collector).

*Physaria Chambersii* is somewhat related to *P. Newberryi* and has been confused with it by several botanists. The technical characters of the two species show that the relationship is not a particularly close one. Both have a broad open sinus at the base of the style and the siliques are large and highly inflated, but here similarity of silique-



characteristics cease. The siliques of *P. Newberryi* have keeled apical margins, truncate base, sinus-crests decidedly angular, style 2–3 mm. long, replum 8–10 mm. long with acute apex and straight-sided valves, whereas in *P. Chambersii* the siliques have rounded sides and apical margins, cordate or nearly truncate base, sinus-crests rounded, style 8–13 mm. long and replum 3–6 mm. long with an obtuse apex. Actually, *P. Chambersii* has a closer relative in *P. australis*. The latter has much smaller coriaceous siliques with closed sinuses of equal depth, whereas *P. Chambersii* has large chartaceous siliques with a deep open apical sinus and a basal sinus which is very shallow or entirely absent. The two species occupy different geographical areas as well.

Variation in the number of ovules in different collections of *P. Chambersii* is puzzling. The ovule-number is consistent for any given collection, but accompanying significant morphological changes apparently have not taken place. Thus, it is possible to find among the collections which are considered to belong to this species a number which have only two ovules in each loculus, a number with four and a few with six. I have not found any variation in number in different siliques from the same plant nor from different plants of the same collection. It would seem from this that a reduction in ovule-number may be independent of other changes in the plant and having once occurred it tends to become fixed or constant. If this is of survival value to the plant, it might be reasonably supposed to be of importance in the origin of new biologically natural entities in the genus.

Var. **membranacea**, var. nov. Herba perennis caespitosa; foliis radicalibus oblanceolatis integris acutis; foliis caulinis integris lineari-oblanceolatis acutis; loculis subreniformibus 1–2 cm. longis, 1–1.5 cm. latis; replo lineari 3–4 mm. longo, 1 mm. lato; stylo persistente 8–12 mm. longo; loculis dispermis.

Caespitose perennial; radical leaves oblanceolate, acute, entire, slender-petioled; cauline entire, linear-oblanceolate, acute; siliques membranaceous, highly inflated, light yellowish, with a deep open sinus above, cordate below, evenly pubescent with appressed stellae; valves subreniform; replum linear, obtuse at apex, 3–4 mm. long, 1 mm. wide; ovules 2 in each loculus.—UTAH: Red Canyon, 16 miles west of Bryce Canyon National Park, Garfield Co., July 6, 1938, *Reed C. Rollins & T. S. Chambers 2448* (G TYPE, R ISOTYPE); Bryce Canyon, Garfield Co., July, 1930, *Goodman & Hitchcock 1567* (NY).

6. *P. DIDYMOCARPA* (Hook.) Gray. Perennial, caespitose, silvery-stellate throughout, stellae branched or simple, often stalked; stems numerous, simple, decumbent, rather leafy for the genus, about 1 dm.



high; radical leaves numerous, obovate, repand or dentate, rarely entire, usually with an angular apex, long-petioled, 1.5–4 cm. long, 8–16 mm. wide; cauline oblanceolate, acute, entire or with an occasional tooth, 1–2 cm. long, 4–8 mm. wide; inflorescence congested, elongating in fruit; sepals pubescent, 6–8 mm. long, 1.5–2 mm. wide, often keeled; petals yellow, spatulate, 10–12 mm. long, 3–4 mm. wide; pedicels spreading, straight or very slightly curved, 8–12 mm. long; siliques didymous, inflated, erect, with deep narrow usually closed apical sinus and similar basal sinus, loosely pubescent with spreading stellae; valves 8–12 mm. long, 6–8 mm. wide; replum obovate to broadly oblong, not constricted, obtuse at apex, 3–4 mm. long, 2–3 mm. broad; style 7–9 mm. long; ovules 4 on each side of replum; seeds marginless, brown, about 2.5 mm. broad, 2–3 in each loculus.

Basal leaves entire, rounded; siliques appressed-pubescent. . . . . Var. *integrifolia*.  
Basal leaves dentate or angular; siliques with a dense spreading pubescence.

Basal leaf-bases lanate, pubescence spreading throughout. . . . . Var. *lanata*.

Basal leaf-bases not lanate, pubescence appressed except on the siliques. . . . . Var. *normalis*.

Var. *NORMALIS* O. Kuntze, Revis. Gen. 1: 35 (1891). *P. didymocarpa* Gray, Gen. Illustr. 1: 162 (1848); Coulter, Man. Rky. Mt. Reg. 26 (1885) in part; Britt. & Brown, Ill. Fl. 2: 135 (1897) in part and ed. 2. 2: 156 (1913) in part; Coulter & Nelson, Man. Cent. Rky. Mts. 217 (1909) in part; Rydb. Fl. Rky. Mts. Adj. Pl. 330 (1917) in part; Payson in Ann. Mo. Bot. Gard. 5: 144 (1918); Rydb., Fl. Pr. Pl. Cent. N. Am. 262 (1933) in part. *Vesicaria didymocarpa* Hook., Fl. Bor.-Am. 1: 49 (1830). *Coulterina didymocarpa* O. Kuntze, Revis. Gen. 2: 931 (1891). *P. macrantha* Blankinship in Mont. Agric. Coll. Sci. Stud. 1, pt. 2: 60 (1905).—Northern Alberta to Wyoming. CANADA: locality uncertain, Rky. Mts., 1858, *Bourgeau* (G, NY); Franklin's Journey (NY). ALBERTA: Kootenay Plains, June, 1908, *S. Brown* 970 (G, NY); jct. north fork and n. branch Saskatchewan R., June, 1908, *S. Brown* 917 (G); Banff, July, 1907, *Butters & Holway* 41 (G, NY); June, 1906, *S. Brown* 123 (G); Bow River Pass, Sept., 1879, *Macoun* 89 (G); Morley, June, 1885, *Macoun* (G, NY); Rky. Mt. Nat. Park, July, 1897, *Van Brunt* 70 (NY); July, 1904, *John Macoun* 64432 (G, NY). MONTANA: Little Belt Mts., Aug., 1896, *Flodman* 596 (NY); Belt Mts., July, 1886, *F. W. Anderson* 411 (NY); Cedar Mt., July, 1897, *Rydberg & Bessey* 4168 (NY); Lima, June, 1895, *Shear* 3406 (NY); Livingston, 1901, *Scheuber* 363 (NY); near Indian Cr., July, 1897, *Rydberg & Bessey* 4166 (NY); Bozeman, May, 1901, *E. J. Moore* (G); Midvale, July, 1903, *Umbach* 305 (G); Granite Butte, Sept., 1912, *Owen Byrnes* 127 (G, isotype of *P. macrantha* Blankin.); Bridger Mts., June, 1897, *Rydberg & Bessey* 4167 (G). WYOMING: Glen Cr., Y. N. Park, June, 1899, *A. & E. Nelson* 5570 (G, NY); near Mammoth Hot Spgs., July, 1893, *Burglehaus* 6318 (NY); Mt. Leidy, Aug., 1897, *Tweedy* 391



(NY); Medicine Mt., Big Horn Co., July, 1936, *L. & R. Williams* 3228 (G, NY).

Plants of *P. didymocarpa* are remarkably uniform from the northernmost portion of its range, extending as far south as northern Wyoming, but specimens from west-central Wyoming show certain transitional stages toward its southern analogue, *P. australis*. These plants, while possessing a broad replum and four ovules in each loculus of the ovary, have appressed stellae on the siliques and entire obtuse basal leaves. The whole series is rather obviously a single line and the segregation of *P. australis* as a distinct entity must have been a comparatively recent evolutionary development. Two varieties of *P. didymocarpa* are recognized in the present treatment and apparently represent two lines of divergence from the parent species. Both have distinctive geographical areas which border the southern margin of the range of variety *normalis*.

Var. *LANATA* A. Nelson in Bull. Torr. Bot. Club **31**: 241. (1904); Coulter and Nelson Man. Cent. Rky. Mts. 217. (1909); Payson in Ann. Mo. Bot. Gard. **5**: 145 (1918). *P. lanata* Rydb. in Bull. Torr. Bot. Club **39**: 322 (1912); Rydb., Fl. Rky. Mts. Adj. Plains 330. (1917).—Central Wyoming. WYOMING: Head of middle fork of Powder River, Big Horn Co., July, 1901, *Goodding* 326 (G, NY ISOTYPES); Wallace Creek, Natrona Co., July, 1894, *A. Nelson* 674 (G); foothills Sheridan-Buffalo, June-July, 1900, *Tweedy* 3585 (NY).

Var. *integrifolia*, var. nov., caespitosa incana; foliis radicalibus integris obovatis; siliquis pubescentibus adpressis.—West-central Wyoming. WYOMING: Grand Canyon of Snake River, Lincoln Co., July 8, 1932, *L. Williams* 809 (G TYPE, NY ISOTYPE); hills east of Afton, Lincoln Co., June, 1923, *Payson & Armstrong* 3825 (G); Adams Ranch, Jacksons Hole, July, 1901, *Merrill & Wilcox* 965 (G); Gros Ventre River, Aug., 1894, *A. Nelson* 927 (G); Headwaters Cliff Creek, Aug., 1900, *C. C. Curtis* (NY).

7. *P. condensata*, sp. nov. Herba perennis caespitosa argentea stellato-pubescentia; caulibus simplicibus brevibus 0.5–1 cm. altis; foliis radicalibus numerosissimis integris obovatis 0.5–1.5 cm. longis, 4–8 mm. latis; foliis caulinis paucis oblanceolatis 5–10 mm. longis, 2–3 mm. latis; pedicellis fructiferis divaricatis rigidis 5–10 mm. longis; siliquis inflatis didymis pubescentibus apice basique cordatis; loculis subsphaeroideis 4–8 mm. diametro; reple obovato 3–4 mm. longo, 2–3 mm. lato; stylo persistente 4–6 mm. longo; seminibus suborbicularibus exalatis 2 mm. diametro; cotyledonibus accumbentibus.

Perennial, caespitose, silvery-stellate throughout; caudex simple or rarely branched, greatly enlarged and invested with old leaf-bases; stems several to many, arising laterally from the caudex beneath a dense rosette of leaves, stellate-pubescent, less than 1 cm. long; basal

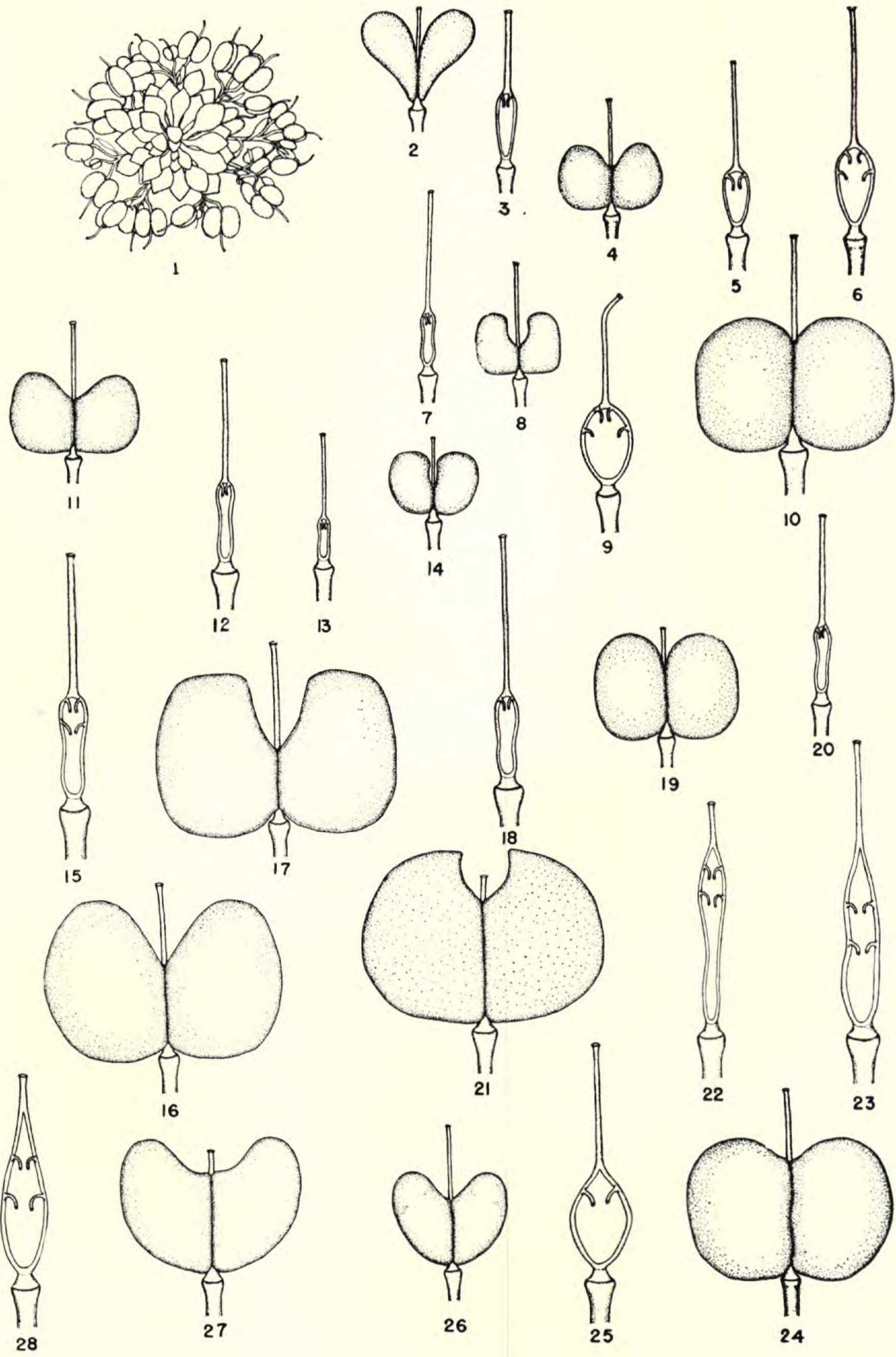


leaves entire, obovate, tapering abruptly to a narrow petiole, silvery from a dense incrustation of appressed stellae, usually acute, 0.5–1.5 cm. long, 4–8 mm. broad; cauline leaves few, oblanceolate, entire, densely stellate, 5–10 mm. long, 2–3 mm. broad; fruiting raceme congested, subumbellate, often almost sessile; pedicels divaricate, straight, 5–10 mm. long; siliques inflated, didymous with a deep sinus at apex and base, pubescent with loosely spreading stellae, inner surface glabrous, loculi 4–8 mm. in diameter; replum obovate, 3–4 mm. long, 2–3 mm. wide; style 4–6 mm. long; ovules 4 in each loculus, 1 or 2 abortive; seeds brown, orbicular, flattened, marginless, 2–4 in each loculus, about 2 mm. in diameter; cotyledons accumbent; flowers unknown.—WYOMING: limy knoll-crest, foothills of Bridger Butte, 3 miles west of Fort Bridger, Uinta County, June 24, 1938, *Reed C. Rollins 2385* (G TYPE, R ISOTYPE).

*Physaria condensata* is analogous in growth-form to *Lesquerella condensata* A. Nelson, by which the specific name is suggested. Both species inhabit unprotected knoll-crests in the Upper Sonoran Life-Zone of southwestern Wyoming, though the latter has a much wider geographic range. *P. condensata*, as shown by its technical characters, is most closely related to *P. didymocarpa*. However, the two species differ so strikingly in growth-habit that they could scarcely be confused either in the field or laboratory. *P. condensata* possesses a dense flat rosette of entire leaves which terminates each sobole or the single caudex, resembling in a general way certain flat-leaved species of *Sedum*. The stems are less than a centimeter long and the whole plant is condensed into a tuft less than five centimeters across. The plant in its normal habitat barely projects above the ground-surface. This is strikingly contrasted with the loose habit of growth, well-developed stems and dentate leaves of *P. didymocarpa*.

8. *P. australis* (Payson), comb. nov. Perennial, caespitose, silvery-stellate throughout, stellae many rayed, rays forked; stems numerous, usually somewhat decumbent, simple, arising laterally, 5–15 cm. long including the fruiting raceme; basal leaves numerous, entire or very rarely with a few scattered teeth, 2–8 cm. long, 5–30 mm. broad, blade obovate to orbicular, obtuse; petiole slender, often narrowly winged; cauline entire, spatulate to oblanceolate, usually obtuse, 1–3 cm. long, 3–8 mm. wide; inflorescence racemose, elongating in fruit; sepals linear-oblong, pubescent; petals spatulate, yellow, about 1 cm. long; pedicels divaricate, slightly sigmoid or nearly straight, 6–12 mm. long; siliques erect, didymous, inflated, pubescent, apical sinus deep, narrow and closed or nearly so, basal sinus similar to apical; valves suborbicular, 6–10 mm. high, 3–6 mm. wide; replum oblong, constricted, 2–3 mm. long; ovules 2 in each loculus; style 4–6 mm.





PHYSARIA

For explanation see end of paper, p. 415.



long; seeds brown, suborbicular, wingless, 2–3 mm. broad.—*P. didymocarpa* (Hook.) Gray var. *australis* Payson in Ann. Mo. Bot. Gard. **5**. 144 (1918); E. H. Graham in Ann. Carneg. Mus. **26**. 220 (1937). *P. didymocarpa* Torr. in Stansbury Expl. & Surv. Great Salt Lake App. D. 284 (1852); Rydb., Fl. Colo. 154 (1906) in part; Coulter & Nelson, Manual Cent. Rky. Mts. 217 (1909) in part; Rydb., Fl. Rky. Mts. Adj. Pl. 330 (1917) in part; Tidestrom in Contrib. U. S. Nat. Herb. **25**: 233 (1925).—Idaho and Wyoming to New Mexico and Utah. IDAHO: Soda Springs, Bannock Co., June, 1920, *E. B. & L. B. Payson* 1701 (G, NY). WYOMING: Sand Creek, Albany Co., June, 1900, *Nelson* 7026 (G, NY); Camel Rock, Albany Co., June 21, 19 ?, *Schwartz & Garner* 51 (G); Dyer's Ranch, Carbon Co., June, 1901, *Goodding* 80 (G); Fort Steele, Carbon Co., May–June, 1901, *Tweedy* 4488 (NY); Bad Water, Fremont Co., June, 1910, *A. Nelson* 19403 (G); Green River, Sweetwater Co., June, 1895, *Shear* 4364 (US), June, 1938, *Rollins* 2241 (G, R); Blacks Fork River, Uinta Co., June, 1937, *Rollins* 1653 (G, NY, R); 3 mi. w. Fort Bridger, Uinta Co., May, 1938, *Rollins* 2229 (G, R); June, 1938, *Rollins* 2387 (G, R); 20 mi. west Big Piney, Lincoln Co., July, 1922, *E. B. & L. B. Payson* 2618 (G, NY). COLORADO: Naturita, Montrose Co., April, 1914, *Payson* 247 (G); Norwood Hill, San Miguel Co., Aug., 1912, *Walker* 490 (G); Paradox, Montrose Co., June, 1912, *Walker* 89 (G, US); Hills about Dolores, June, 1892, *C. S. Crandall* (G); 10 mi. so. Montrose, Montrose Co., May, 1938, *Rollins* 2134 (G); 8 mi. w. Grand Junction, Mesa Co., May, 1938, *Rollins* 2176 (G, R); 20 mi. no. Rifle, Rio Blanco Co., May, 1938, *Rollins* 2209 (G, R); dry hills near Meeker, Rio Blanco Co., May, 1938, *Rollins* 2220 (G, R); Durango, June, 1898, *Crandall* (NY); Mancos, June, 1898, *Baker, Earle & Tracy* 75 (G, US); Mesa Verde Park, May, 1925, *A. Nelson* 10425 (NY). NEW MEXICO: Aztec, April, 1899, *Baker* 356 (G, NY, US); vicinity of Farmington, San Juan Co., July, 1911, *Standley* 7129 (US). UTAH: Logan Canyon, Cache Co., April, 1911, *C. P. Smith* 2331 (NY), May, 1934, *Bassett & Ruth Maguire* 15956 (G); Wahsatch Mts., July, 1869, *S. Watson* 83 (NY); Orangeville, June, 1894, *M. E. Jones* 5464 (US); Price, June, 1900, *Stokes* (NY); Theodore, Uintah Co., May, 1908, *M. E. Jones* (NY); 47 mi. so. Moab, June, 1933, *B. Maguire et al.* 5809 (US); Flaming Gorge, Daggett Co., May, 1932, *L. Williams* 458 (G, NY); La Sal Mts., July, 1911, *Rydberg & Garrett* 8573 (NY); June, 1913, *M. E. Jones* (NY); 4 mi. w. Willow Creek, Uintah Co., June, 1937, *Rollins* 1708 (G, R).

A careful examination of numerous specimens of Payson's variety *australis* has revealed a number of fundamental characteristics which indicate its distinctness as a separate species from *P. didymocarpa*. Chief among these is a reduced number of ovules in each loculus of the ovary. In *P. didymocarpa* there are four<sup>1</sup> ovules in each of the two

<sup>1</sup> Figs. 9 and 10, tab. XVI, Hook. Fl. Bor.-Am. must certainly be in error as to the number of ovules. I have examined the siliques of over thirty collections of this



loculi. Often one and sometimes two ovules abort, consequently only two or three seeds mature on each side of the replum. *P. australis* has only two ovules in each loculus and the funiculi are at the very apex of the replum. Usually one of the two ovules aborts, leaving only one which matures. Equally consistent but possibly less fundamental is the difference in the nature of the replum of these species. *P. australis* has a very narrowly linear constricted replum which is less than 1 mm. wide, whereas the replum of *P. didymocarpa* is oblong to obovate and 2–3 mm. wide. When these constant differences are added to those pointed out by Payson the specific nature of *P. australis* becomes apparent.

9. *P. GRAHAMII* Morton. Perennial, caespitose, densely pubescent throughout with spreading stellae; stems simple, somewhat decumbent, about 1.5 dm. long; basal leaves numerous, broadly oblanceolate to broadly spatulate, obtuse, irregularly pinnatifid, 10–15 cm. long, about 3 cm. broad, distal lobes large and variable; cauline few, dentate or rarely entire; pedicels divergent, 5–15 mm. long; sepals linear-oblong, pubescent, about 5 mm. long; petals yellow, spatulate, 6–8 mm. long; siliques erect, didymous, inflated but not highly so, shallow sinus below, deep sinus above; replum linear-oblong, somewhat constricted, ovules 2 on each side; style 6–8 mm. long; mature seeds unknown.—Morton in E. H. Graham in Ann. Carneg. Mus. **24**: 220 (1937).—UTAH: Chandler Canyon, Uinta Basin, Uintah County, Aug. 3, 1935, *Graham 9976* (US TYPE).

The type of this species is not altogether satisfactory because the fruits are very immature. Its distinctiveness rests upon the fact that the whole plant is covered with very loose spreading stellae and that the large basal leaves are deeply lobed along the margins. *P. Grahamii* is at present known only from the type collection.

10. *P. BRASSICOIDES* Rydberg. Perennial, caespitose, silvery-stellate throughout, stellae with forked rays; stems several to numerous, rather stoutish for the genus, simple, arising laterally, 5–15 cm. long including the fruiting raceme; basal leaves numerous, thick, scurfy above, repand or rarely entire, 2–6 cm. long, 1–2.5 cm. broad, blade orbicular to obovate, petiole somewhat winged; cauline few, oblanceolate to broadly spatulate, obtuse or approaching acuteness, entire, 1–2 cm. long, 3–5 mm. wide; sepals linear-oblong, 6–8 mm. long, about 1 mm. wide; petals yellow, spatulate, about 1 cm. long, 3–4 mm. wide; pedicels divergent, straight or somewhat curved, 5–10 mm. long; si-

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species and consistently find four ovules on each side of the replum. The drawings are also in error as to the acute apex of the replum. This is characteristic of *P. Geyeri* and is probably taken from Douglas' plants which Hooker cited. The apical angle of the replum of *P. didymocarpa* is decidedly obtuse.



liques didymous, erect, cordate, inflated but not greatly so, loosely but densely pubescent with spreading stellae, obtuse or with an obscure sinus at base, apical sinus deep and broad, valves 6–8 mm. high; replum linear-oblong, constricted, 3–4 mm. long, about 1 mm. wide; ovules 2 in each loculus; style 4–5 mm. long; seeds brown, 2–3 mm. broad.—Bull. Torr. Bot. Club **29**: 237 (1902); Peterson, Fl. Neb. 62 (1912); Rydb., Fl. Rky. Mts. Adj. Pl. 331 (1917); Payson in Ann. Mo. Bot. Gard. **5**: 145 (1918); Rydb., Fl. Pr. Pl. Cent. N. Am. 362 (1932). *P. didymocarpa* Britt. & Brown, Ill. Fl. ed. 2. **2**: 156 (1913) in part; Bergman, Fl. N. Dak. 191 (1918); Winter in Contrib. Bot. Surv. Neb. n. s. **10**: 71 (1936).—NORTH DAKOTA: Medora, July 17, 1898, *L. R. Waldron* (NDA, NY); June 19, 1910, *H. F. Bergman* (NDA); Gorham, McKenzie Co., May, 1938, *E. C. Moran* 399 & 400 (G). SOUTH DAKOTA: cultivated at Brookings from seed collected in badlands, *Th. A. Williams* (G). NEBRASKA: canyon south of Scott's Bluff, Scott's Bluff Co., July, 1891, *Rydberg* 24 (NY TYPE, US ISOTYPE); badlands, 1853–4, *F. V. Hayden* (NY). WYOMING: 1 mi. northwest of Hulett, Crook Co., May, 1935, *Owenby* 610 (NY, R).

An inhabitant of bluffs and badlands in the western plains region, *P. brassicoides* is one of the least known species of the genus *Physaria*. Its affinities are with *P. didymocarpa* var. *lanata* on the one hand and *P. vitulifera* on the other. The dense loose whitish vestiture of the siliques immediately suggests *P. didymocarpa* and its variety *lanata*, but the replum is constricted, the ovules number two in each cell and the base of the silique is almost devoid of a sinus like that of *P. vitulifera*. From the latter species it differs in having very much larger, almost entire thickish basal leaves, larger more highly inflated obpyriform siliques and a longer replum. Little difficulty should be experienced in placing specimens of this rather unique species.

11. *P. VITULIFERA* Rydberg. Perennial, caespitose, silvery stellate-pubescent throughout; stellae with numerous branched rays; stems numerous, usually decumbent, arising laterally, simple, rather coarse, 1–2 dm. long including fruiting raceme; basal leaves numerous, pandurate or merely obovate, obtuse, margins deeply and broadly incised or rarely almost entire, 3–6 cm. long, 1–2 cm. broad; cauline entire, oblanceolate to spatulate, often somewhat acute, 3–6 mm. broad; inflorescence congested, elongating in fruit; sepals oblong, pubescent, 6–8 mm. long, 1.5–2 mm. wide; petals yellow, spatulate, about 1 cm. long, 3–4 mm. wide; pedicels sigmoid, the end usually curving upward; siliques didymous, often rigid, inflated, somewhat angular, pubescent with loose spreading stellae, obtuse or truncate below, apical sinus broad, open and deep; valves 5–6 mm. high, 3–4 mm. broad; replum oblong, often constricted, 2–3 mm. long, less than 1 mm. wide, 2 ovules on each side; style 5–7 mm. long; seeds 1–2 in each loculus,



brown, about 2.5 mm. broad, wingless.—Bull. Torr. Bot. Club **28**: 278 (1901); Rydb., Fl. Colo. 154 (1906); Coulter & Nelson, Man. Cent. Rky. Mts. 218 (1909); Rydb., Fl. Rky. Mts. Adj. Pl. 330. (1917); Payson in Ann. Mo. Bot. Gard. **5**: 145 (1918). *P. didymocarpa* Clements & Clements, Rky. Mt. Fls. 25 (1914) in part. *P. didymocarpa*  $\beta$  *contractoreplum* O. Kuntze, Revis. Gen. Pl. **1**: 35 (1891).—COLORADO: without locality, Sept., 1874, O. Kuntze 3058 (NY isotype of *P. didymocarpa*  $\beta$  *contractoreplum*); Idaho Springs, Aug., 1895, Rydberg (NY TYPE); June, 1916, Clokey 2753 (NY); Aug., 1895, Shear 3269 (NY, US); near Golden, June, 1918, Churchill (G); July, 1917, E. L. Johnston 1019 (G); April, 1892, Crandall 45 (NY, US); May, 1920, Duthie & Clokey 3777 (Cl, G, NY, US); Morrison, Jefferson Co., July, 1920, Clokey 3776 (Cl); near Boulder, July, 1902, Tweedy 5068 (NY); Clear Creek-Middle Park, 1861, Parry 101 (G, NY); Platte River, Evans, June, 1910, E. L. Johnston 633 & 633b (NY).

*P. vitulifera* has two close relatives in *P. floribunda* and *P. Osterhoutii*. Its position appears to be somewhat intermediate between these two species both morphologically and geographically. The plant ranges along the western edge of the plains and in canyons and valleys toward the interior of the central Rocky Mountains of Colorado. *P. Osterhoutii* occurs northwest and *P. floribunda* occurs to the south and west of this area.

The basal leaves of *P. vitulifera* are similar to those of *P. floribunda*, but they are nearly always obtuse instead of acute and obovate instead of broadly oblanceolate. The fruits are angular, rigid in appearance and not highly inflated. Stellae on the siliques are not appressed as on the foliage, but, as in *P. Osterhoutii*, spread at almost right angles from it. As a biological entity, the boundaries of *P. vitulifera* are seemingly well defined; however, recent connections with its relatives are strongly indicated.

12. *P. OSTERHOUTII* Payson. Perennial, caespitose, silvery-stellate throughout, rays of stellae usually forked; caudex simple or branched; stems slender, numerous, erect or somewhat decumbent, arising laterally, simple, 8–15 cm. long including the raceme; basal leaves oblanceolate, often hastate, incised or with broad teeth along the petiole, rarely entire, 2–5 cm. long, 8–15 mm. wide; cauline linear-oblanceolate, acute, entire or rarely with a few teeth, 1–2 cm. long, 2–3 mm. wide; inflorescence congested, flowers numerous; sepals linear-oblong, yellowish, pubescent, 5–7 mm. long, about 1 mm. wide; petals yellow, spatulate, 8–10 mm. long, 3–4 mm. wide; pedicels recurved in fruit, 1–1.5 cm. long; fruiting raceme congested, 4–8 cm. long; siliques pendant, base truncate or obtuse, apex deeply emarginate; valves inflated but not highly so, 5–7 mm. long, 4–5 mm. broad,



rather loosely stellate-pubescent; replum oblong or slightly broader, obtuse at apex, 2–3 mm. long; style 4–5 mm. long; ovules 2 on each side of replum; seeds orbicular, marginless, 1–2 in each loculus, about 2 mm. broad.—Ann. Mo. Bot. Gard. 5: 146 (1918).—COLORADO: Kremmling, Grand Co., June, 1907, *Osterhout 3477* (NY ISOTYPE 2 sheets); Sulphur Springs, July, 1907, *F. E. Clements* (NY).

This species is very closely related to *P. vitulifera*, differing only in a few characters which appear to be of relatively minor importance. *P. Osterhoutii* has more slender nearly entire basal leaves which are acute instead of obtuse as in *P. vitulifera*, more numerous stems and a pendant instead of erect silique. The distinctness of the entity as a species must remain in doubt at present. Certainly a larger series of specimens together with accurate field data are needed to establish the range of variability and precise relationships of this unit. Its known range is entirely in north-central Colorado.

13. *P. ACUTIFOLIA* Rydberg. Perennial, caespitose, silvery stellate-pubescent throughout, stellae with branched rays; stems several to numerous, decumbent, simple, slender, 5–10 cm. long including fruiting raceme; basal leaves oblanceolate or broader, acute, entire or with one or two broad teeth, 2–3.5 cm. long, 5–10 mm. wide, blades sometimes triangular; cauline few, oblanceolate, entire, acute, 1–1.5 cm. long, 2–4 mm. wide; inflorescence congested, elongating moderately in fruit; sepals linear, 5–7 mm. long, 1 mm. wide; petals yellow, spatulate, often somewhat truncate at apex, 8–10 mm. long, 2–3 mm. wide; pedicels spreading, somewhat sigmoid, 5–8 mm. long; siliques erect, didymous, inflated, slightly cordate at base or nearly obtuse, apical sinus broad and deep; valves suborbicular, 4–5 mm. wide, 6–8 mm. high; replum obovate to slightly longer, obtuse at apex, rarely somewhat constricted toward base, about 3 mm. long, about 1.5 mm. wide; style 5–7 mm. long; ovules 2 on each side of replum; seeds orbicular, brown, only slightly flattened, about 2 mm. broad, 1–2 in each loculus.—Bull. Torr. Bot. Club. 18: 279 (1901); Rydb., Fl. Colo. 154 (1906) in part; Fl. Rky. Mts. Adj. Pl. 331 (1917) in part; Payson in Ann. Mo. Bot. Gard. 5: 145 (1918). *P. floribunda* Nelson, Coulter & Nelson Man. Cent. Rky. Mts., 218 (1909) in part.—COLORADO: Grand Junction, Mesa Co., June, 1892, *A. Eastwood* (NY TYPE); South Park, *Wolf & Rothrock 642* (G); Steamboat Springs, Routt Co., July, 1903, *Goodding 1623* (G, NY, US); Ruxton Ridge, Pikes Peak, July, 1901, *F. E. & E. S. Clements 97* (G, NY, US); 10 mi. east of Sapinero, Gunnison Co., May, 1938, *Rollins 2106* (G, R); 5 mi. east of Parlin, Gunnison Co., May, 1938, *Rollins 2088* (G, R); Caldwell Cr., Rio Grande Nat. Forest, Mineral Co., June, 1911, *Murdoch 4542* (NY).

*P. acutifolia* belongs to the *floribunda-Osterhoutii-vitulifera* group, but differs from all in having smaller entire acute leaves, slender short



stems and an obovate unconstricted replum. Of this group, *P. floribunda* stands closest to *P. acutifolia* and it is quite possible that further investigation will show them to be varieties or phases of a single species. More field-work in the area where these species occur will be necessary before the case can be fully clarified. At present it seems that the dissected basal leaves, descending or obliquely spreading pedicels, greater size and linear-oblong constricted replum of *P. floribunda* are sufficient to distinguish it from its near relative. *P. acutifolia* is found at middle elevations in the central Rocky Mountains of Colorado and is known to be particularly abundant in the Gunnison Basin.

14. *P. FLORIBUNDA* Rydberg. Perennial, caespitose, silvery stellate-pubescent throughout, stellae with branched rays; stems numerous, simple, arising laterally, decumbent or erect, 1–2 dm. long including the fruiting raceme; radical leaves broadly oblanceolate, pinnatifid or merely dentate, rarely almost entire, 4–8 cm. long, 1–2 cm. wide, terminal lobe acute or obtuse but not rounded, petiole usually winged; cauline spatulate to linear-oblanceolate, acute, entire or rarely few-toothed, 1–3 cm. long, 3–6 mm. wide; inflorescence loosely racemose, greatly elongating in fruit; sepals linear-oblong, 5–7 mm. long, 1–2 mm. wide; petals yellow, spatulate, 9–11 mm. long, about 3 mm. wide; pedicels spreading or somewhat recurved, usually sigmoid, slender, 6–12 mm. long; siliques erect divergent or nearly pendant, didymous, inflated but not greatly so, obtuse or slightly cordate at base, deeply and broadly notched above, valves 4–6 mm. high, 3–5 mm. wide; replum linear-oblong, constricted, 2.5–4 mm. long, less than 1 mm. wide, obtuse at apex, ovules 2 on each side; style 5–8 mm. long; seeds brown, orbicular, about 2 mm. broad, marginless, 1–2 in each loculus.—Bull. Torr. Bot. Club **18**: 279 (1901); Fl. Colo. 154 (1906) in part; Coulter & Nelson, Man. Cent. Rky. Mts. 218 (1909) in part; Rydb., Fl. Rky. Mts. Adj. Pl. 330 (1917); Payson in Ann. Mo. Bot. Gard. **5**: 146 (1918).—COLORADO: west slope LaVeta Pass, Costilla Co., *McKelvey* 4787 & 4789 (G); *Bethel, Willey & Clokey* 4130 (Cl, G); Sangre de Cristo Creek, July, 1900, *Rydberg & Vreeland* 6135 (NY TYPE); *Rydberg & Vreeland* 6136 (NY); Cimarron, Gunnison Co., June, 1901, *Baker* 38 (G, NY, US); 3 mi. east of Sapinero, Gunnison Co., May, 1938, *Rollins* 2108 (G, R); Wolcott, July, 1898, *Shear & Bessey* 5295 (NY, US); Glenwood Springs, Garfield Co., June, 1920, *Osterhout* (Cl); Ruxton, Pikes Peak, 1896, *Clements* 160 (NY); Bostwick Park, Montrose Co., Aug., 1937, *Rollins* 1983 (G, R); July, 1917, *Payson* (US); Ridgway, Ouray Co., June, 1924, *E. B. & L. B. Payson* 3832 (G); 3 mi. ne. of Cedaredge, Delta Co., May, 1938, *Rollins* 2150 (G, R); 10 mi. n. of Mesa, Mesa Co., May, 1938, *Rollins* 2194 (G, R); near Mesa, Mesa Co., May, 1938, *Rollins* 2197 (G, R). NEW MEXICO: 10 miles east of Taos, Taos Co., July, 1938, *Rollins & Chambers* 2414 (G, R).